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Larval Duration, Settlement, and Larval Growth Rates of the Endangered Tidewater Goby (*Eucyclogobius newberryi*) and the Arrow Goby (*Clevelandia ios*) (Pisces, Teleostei)

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Abstract.—The early life history of the federally endangered Tidewater Goby (*Eucyclogobius newberryi*) and its sister species the Arrow Goby (*Clevelandia ios*) has been poorly documented to date. Both are endemic to estuarine habitats throughout the California coast, however, habitat use differs between these two species. The Arrow Goby is commonly found in fully marine tidal bays and mudflats. The Tidewater Goby, however, prefers lagoons with some degree of seasonal isolation from the sea. Here, we used otoliths to examine the larval duration, size at settlement, and growth rates of newly settled gobies collected from 18 estuaries in California. The Tidewater Goby had a larval duration that was ~2 days shorter than the Arrow Goby (23.95 vs. 26.11 days, respectively), but a larger size at settlement based on back-calculated size (12.38 vs. 10.00 mm SL) due to a faster larval growth rate (2.86 vs. 2.60 μm/day^{-1}). There are several reasons that could explain these differences in larval traits, such as differences in temperature or food resources between the two estuary types, or the faster, annual life cycle of the Tidewater Goby relative to the Arrow Goby.

Many fish species inhabit estuarine habitats during their early life history. These habitats are quite variable, with some remaining open to the ocean year round and others typically closing seasonally. Species that inhabit seasonally closing estuaries may exhibit different larval traits than those that inhabit permanently open estuaries, and these traits may contribute to genetic isolation by limiting dispersal (Bilton et al. 2002, Watts and Johnson 2004). For example, Dawson et al. (2002) found genetic evidence of limited dispersal in the Tidewater Goby (*Eucyclogobius newberryi*), which inhabits seasonally closed estuaries, whereas its sister species the Arrow Goby (*Clevelandia ios*), which inhabits open systems, lacked regional genetic divergence. This difference is likely due to greater marine larval dispersal and gene flow between populations of arrow gobies. Larval duration has long been thought to influence dispersal, and differences in larval duration could confound this interpretation.

Closed estuaries experience greater seasonal variation in environmental conditions than is seen in estuaries perennially open to marine influence, and such variation is known to significantly influence larval development (McCormick and Molony 1995, Green and Fisher 2004). Along the California coast, many estuaries are partially or completely isolated from tidal influence either seasonally or episodically (Jacobs et al. 2011). Opening or "breaching" is usually a function of streamflow (Rich and Keller 2013), which is driven by seasonal precipitation. Isolation, or closure, occurs when a sand bar or raised beach berm impounds systems during periods of lowered "summer" streamflow, creating variable salinity. Such dynamic lagoonal systems are a product of the Mediterranean climate that characterizes California. Similar lagoonal processes are known to occur in other regions of the globe with similar climate (Jacobs et al. 2011).

The federally endangered Tidewater Goby is a California endemic that occurs in estuaries that experience seasonal or episodic closure (Swift et al. 1989). The Tidewater Goby is a small benthic fish that seldom exceeds 55 mm standard length (SL) (Miller and Lea 1972). Lagoons with seasonally closing stream mouths on the outer coast are the typical Tidewater Goby habitat, although they also occupy or historically occupied, naturally closing, tide-gated, or marginal pond habitats around Humboldt, Tomales, and San Francisco Bays (Swift et al. 1989, Moyle 2002, U.S. Fish and Wildlife Service 2005). This species exhibits local genetic divergence at a finer geographic scale than any other Pacific coast vertebrate (Barlow 2002, Dawson et al. 2002, Earl et al. 2010). Its preference for small and isolated estuaries is one of the main reasons why it is predisposed to local extirpation (Lafferty et al. 1999a,b).

Dispersal of the Tidewater Goby is associated with high streamflow events (Lafferty et al. 1999a,b), which cause breaching of the estuary mouth, permitting dispersal (Earl et al. 2010). Breaching events occur most frequently during winter months when reproduction is limited and larvae are generally absent. As confirmed by genetic divergence, marine larval dispersal appears to be extremely limited, if it occurs at all (Barlow 2002, Dawson et al. 2002, Earl et al. 2010). This conclusion is supported by the work of Hellmair and Kinziger (2014), which showed that small tidewater gobies (<25 mm total length) experience higher mortality rates than larger individuals (>25 mm) when salinity was raised from 6‰ to 26‰. Presumably this intolerance to seawater in young tidewater gobies is related to the isolated nature of their lagoonal habitats during the summer peak reproductive months (Swenson 1999). Thus, dispersal appears limited to adult movement over sandy substrate following breaching events (Earl et al. 2010).

The Arrow Goby is the sister species to the Tidewater Goby (Dawson et al. 2002), and it ranges from Bahia Magdalena, Baja California Sur (C. Swift, pers. comm.) to British Colombia (Miller and Lea 1972). Similar to the Tidewater Goby, the Arrow Goby is a small benthic fish that rarely exceeds 60 mm SL (Miller and Lea 1972, Hart 1974). It prefers more open, fully tidal estuaries and mudflats, which are typically cooler and higher in salinity. This preference for open estuaries is thought to facilitate marine larval dispersal.

Here, we compare the early life history of the Arrow Goby and the Tidewater Goby collected from eighteen California estuaries. Larval traits were determined from daily bands and settlement marks in lapillar otoliths of recently settled gobies. Larval duration, size at settlement, and pre-settlement growth rates were compared between the two species.

Materials and Methods

Study Sites

Gobies were collected from eighteen estuaries in California (Fig. 1). Sites were chosen based on the presence of healthy and abundant populations of the Arrow Goby or Tidewater Goby, in addition to their mouth dynamics (closed vs. open estuary mouth). The Tidewater Goby was collected at ten seasonally closing estuaries: Ten Mile River (39°32′43.86″N, 123°45′25.04″W); Salmon Creek (38°21′10.87″N, 123°03′57.19″W); Rodeo Lagoon (37°49′54.41″N, 122°31′43.31″W); San Gregorio (37°19′14.29″N, 122°24′03.38″W); Moore Creek (36°57′4.50″N, 122°03′29.85″W); San Luis Obispo Creek (35°11′13.35″N, 120°43′33.47″W); Santa Ynez River (34°41′30.57″N, 120°35′00.70″W);

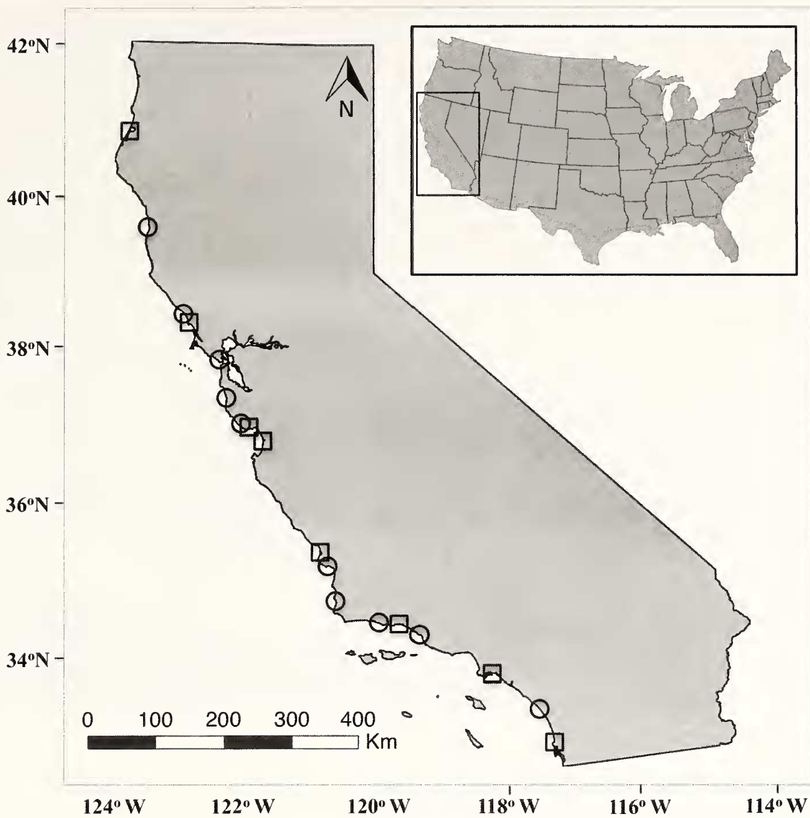

Fig. 1. Map of the 18 study sites located along the California coastline. The Arrow Goby (squares) was collected at 8 sites, and the Tidewater Goby (circles) was collected at 10 sites.

Arroyo Burro Lagoon (34°24′11.77″N, 119°44′35.12″W); Santa Clara River (34°14′07.19″N, 119°15′27.46″W); and Las Flores Marsh (33°17′25.79″N, 117°27′53.91″W). The Arrow Goby was collected at eight estuaries that are typically fully tidal: Arcata Bay (40°51′30.57″N, 124°06′00.08″W); Bodega Bay (38°18′59.42″N, 123°02′43.12″W); San Lorenzo River (36°57′56.41″N, 122°00′45.46″W); Elkhorn Slough (36°48′40.14″N, 121°44′38.77″W); Morro Bay (36°57′56.41″N, 122°00′45.46″W); Carpinteria Salt Marsh (34°23′52.97″N, 119°32′16.72″W); Colorado Lagoon (33°45′10.52″N, 118°07′47.37″W); and Los Peñasquitos (32°55′57.84″N, 117°15′29.11″W). Due to the differences in habitat preference of the Arrow Goby and Tidewater Goby, none of the eighteen study sites had both species present at the time of collection.

Collection Methods

Larval, transitional, and recently settled gobies (Fig. 2) were collected between August and October of 2011. Both species were collected using a 3.7 x 1.2 m beach seine with a 1.6-mm mesh, and in some cases, a one-man push net with 1.6-mm mesh (Strawn 1954). The Arrow Goby was collected at low tide in all eight study sites. The ten study sites where the Tidewater Goby was collected were all completely closed to marine tidal influence at the time of collection. Once collected, the fishes were euthanized and preserved in 95% ethanol.

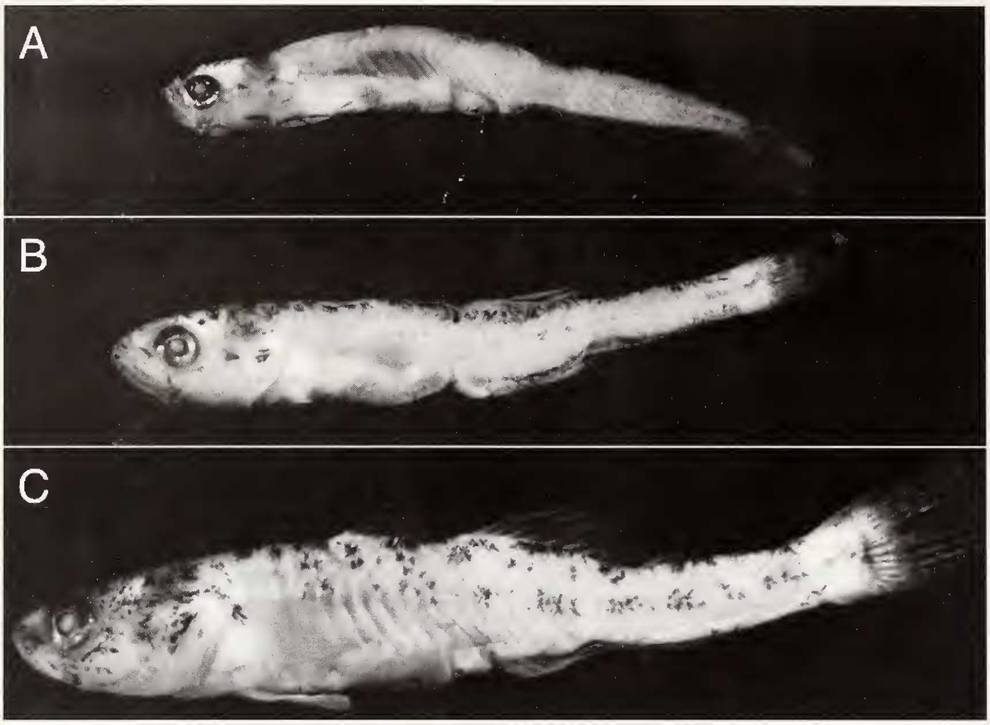

Fig. 2. Photos showing the rapid development of the Tidewater Goby, exhibiting the transition from (A) a 20-day-old postflexion larva (9.3 mm SL), to (B) a 25-day-old transitional juvenile captured prior to settlement (10.8 mm), and (C) a 34-day-old settled juvenile (13.7 mm).

Otolith Analysis

Otoliths were used to measure larval traits of the study species. Otoliths have been used for these purposes in a wide variety of fishes, including many species in the family Gobiidae (Sponaugle and Cowen 1994, Hernaman et al. 2000, Radtke et al. 2001, Yamasaki and Maeda 2007, Wilson et al. 2009, Samhouri et al. 2009). Both the sagittal and lapillar otoliths were extracted from all individuals using standard techniques (Brothers 1987, Hellmair 2010) and placed in immersion oil for >30 days to clear (Samhouri et al. 2009). For both species, lapilli were used because they were clearer and easier to interpret than sagittae, and they did not require sectioning or polishing. Lapilli were read whole from images on a computer monitor that were captured by a digital camera mounted on a compound microscope at 200× magnification, with a polarizing filter placed between the light source and the first stage. Increment measurements were made along the longest axis, from the core to the outermost complete ring using Image-Pro Plus image analysis software.

Larval duration, size at settlement, and growth rates were estimated from the otoliths. Previous work has validated daily otolith increment deposition in the Tidewater Goby (Hellmair 2010), and increments were assumed to be daily in the Arrow Goby. Settlement was recorded in the otolith structure as a distinct transition in increment widths (Fig. 3), as noted in other gobies by Sponaugle and Cowen (1994). Larval duration was determined from a count of the rings from the hatch mark (first band from otolith core) to the settlement mark. Average pre-settlement growth rates were estimated as average

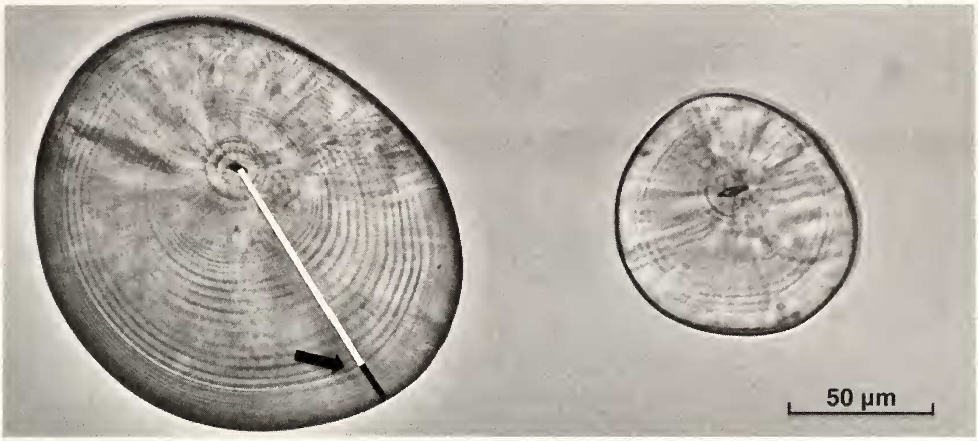

Fig. 3. Lapillar otolith of a juvenile Tidewater Goby (A), and a larval Tidewater Goby (B) with visible daily bands viewed at 200 x magnification. The black arrow indicates the settlement band. The white line indicates pre-settlement bands, and the black line represents post-settlement bands.

increment width between the hatch mark and the settlement mark (McCormick and Molony 1995). All otoliths were read twice by one person (B.T. Spies), and all unclear and abnormally shaped otoliths were discarded. If the two readings were more then 10% different, then that otolith was not included in any analysis. If the two readings were less than 10% different but not the same, then the second reading was used for the analysis.

Data Analysis

To validate that the presumed settlement mark actually corresponded to settlement, the number of presumed post-settlement bands was regressed against body length for both species. The x-intercept of the linear regression equation estimates size at settlement, which was compared to the size of fish known to have recently settled based on their morphology. Further regression analyses examined the relationship between body length and age (days) to determine whether otolith measurements provide accurate proxies of somatic traits (Booth and Parkinson 2011). Back calculation was used to estimate body size at settlement for each fish using the equation calculated by ordinary least square linear regression of body size (mm SL) on otolith radius, of the form $L = mx + b$; where L represents the body length, m represents the slope, x represents the otolith radius at settlement, and b represents the y-intercept. A nested ANOVA with the factors Species (fixed effect) and Site nested within species (random effect) was used to test whether larval traits differed between species and collection sites.

Results

Otolith-based estimates of larval traits appeared to be appropriate for both the Tidewater Goby and Arrow Goby due to the fact that body length was tightly related to age as estimated from otoliths (Arrow Goby: $r^2=0.75$, $n=317$; Tidewater Goby: $r^2=0.71$, $n=406$; Fig. 4). The number of post-settlement otolith bands and body length were also tightly related (Arrow Goby: $r^2=0.79$; Tidewater Goby: $r^2=0.73$) and the fitted lines predicted realistic sizes at settlement (Fig. 5). This result indicates that the distinguishable transition zone in the otolith is the settlement band (Fig. 3A), and that all bands between the core and the settlement mark indicate the larval duration (Sponaugle and Cowen

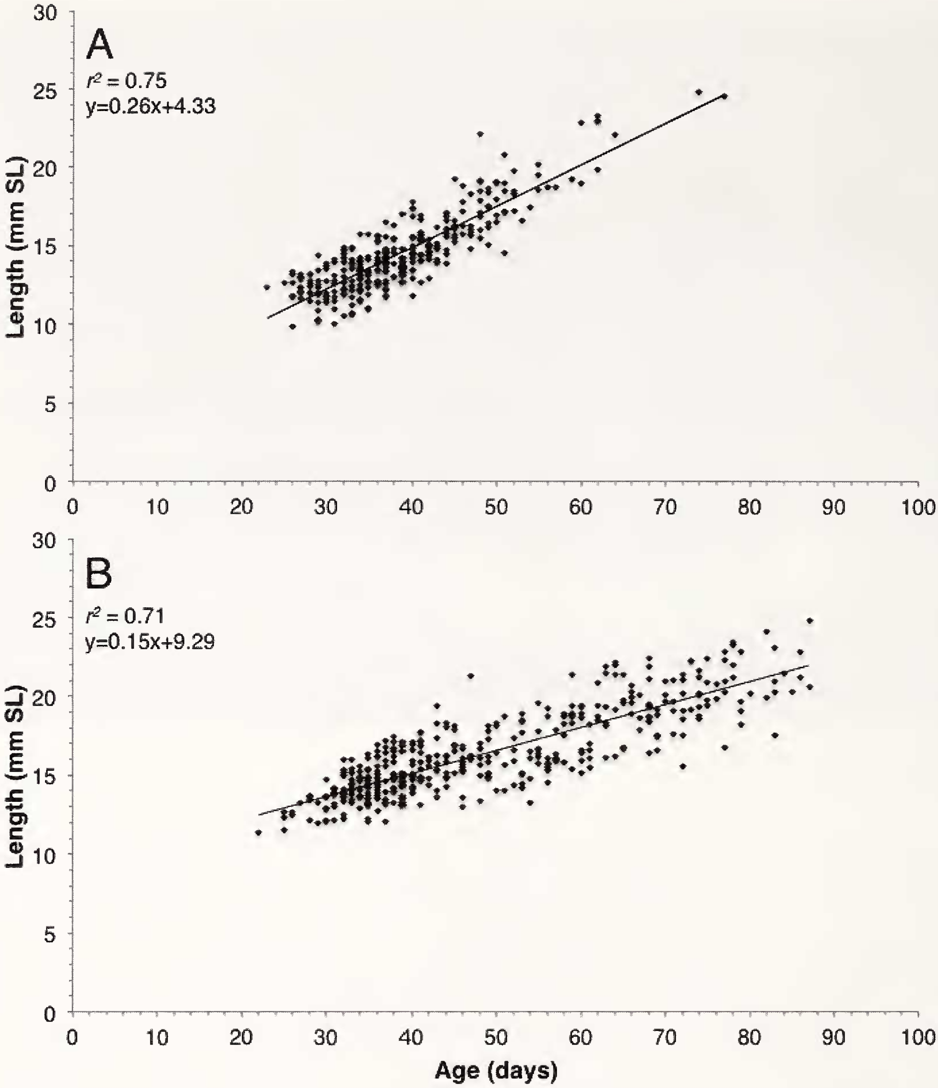

Fig. 4. Relationship between body length and age for the Arrow Goby (A) and Tidewater Goby (B).

1994). Otolith radius was a good proxy for body length, as indicated by a strong linear relationship between body length and otolith radius (Arrow Goby: r^2=0.80; Tidewater Goby: r^2=0.78; Fig. 6). Based on back-calculation, mean ± SD size at settlement was 11.45 ± 0.23 mm SL for the Tidewater Goby and 9.32 ± 0.63 mm for the Arrow Goby, slightly smaller than the estimates of size at settlement based on the x-intercept of the regressions of post-settlement age on size (Fig. 5, Table 1).

The Arrow Goby had a significantly longer larval duration ($F_{1,705}$=227.3, p<0.0001), larger otolith radius at settlement ($F_{1,705}$=28.4, p<0.0001), and slower larval growth rates ($F_{1,705}$=399.8, p<0.0001) than the Tidewater Goby (Table 1). Size at settlement (back calculated) of the Tidewater Goby was significantly larger than that of the Arrow Goby ($F_{1,705}$=5360.1, p<0.0001). All larval traits varied significantly among sites for both species (larval duration: $F_{16,705}$=42.5, p<0.0001; otolith radius at settlement: $F_{16,705}$=43.9,

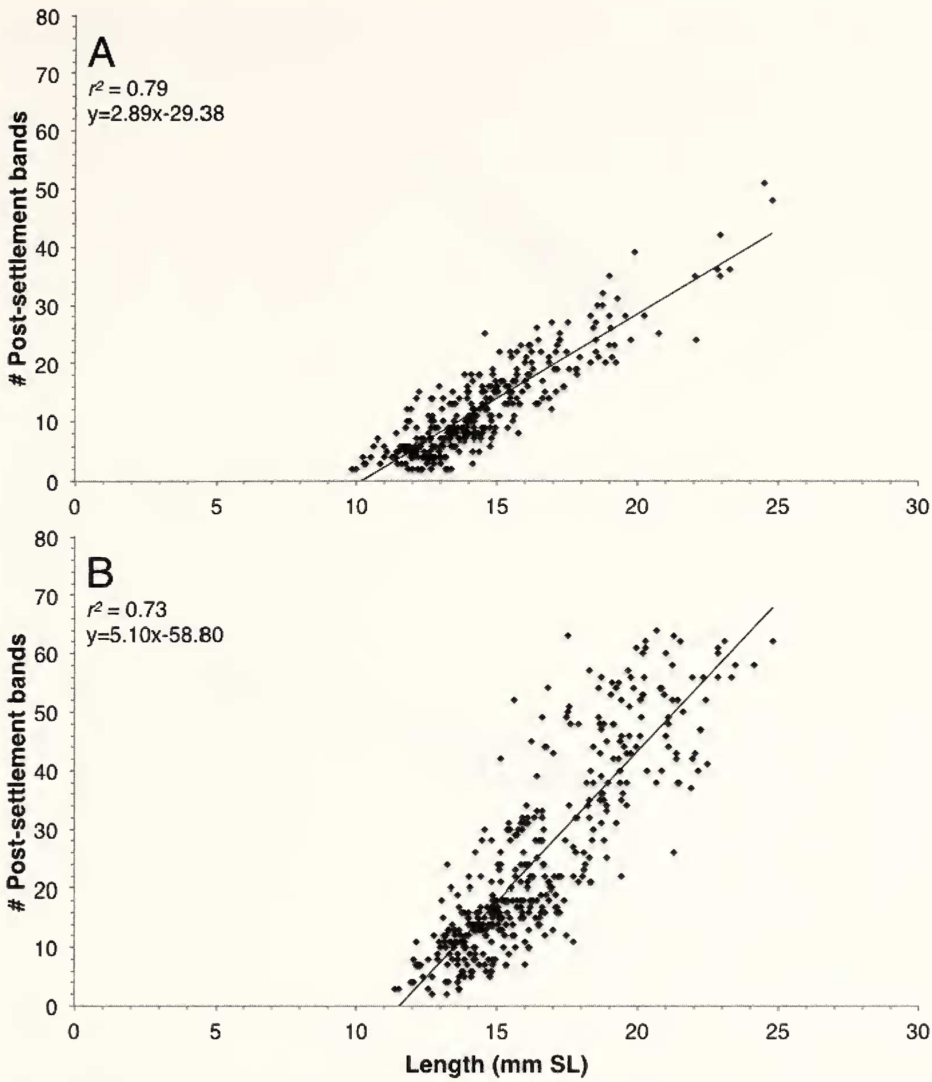

Fig. 5. Relationship between post-settlement age and body length for the Arrow Goby (A) and Tidewater Goby (B).

$p<0.0001$; pre-settlement growth rate: $F_{16,705}=33.53$, $p<0.0001$; back calculated body size at settlement: $F_{16,705}=25.9$, $p<0.0001$).

Discussion

Analysis of lapillar otoliths revealed that larval duration, size at settlement, and pre-settlement growth rates of the two sister species, the Arrow Goby and Tidewater Goby, were statistically different, though not dramatically different. The similarity between the two species in larval duration is somewhat surprising given known differences in their habitat usage and methods of dispersal. Despite inhabiting two different kinds of estuaries, "open" versus "closed", and dispersing as larvae (Arrow Goby) versus adults (Tidewater Goby), the duration of the larval phase was only 8% shorter in the Tidewater Goby. Due to faster larval growth rates, the Tidewater Goby settled at larger size than

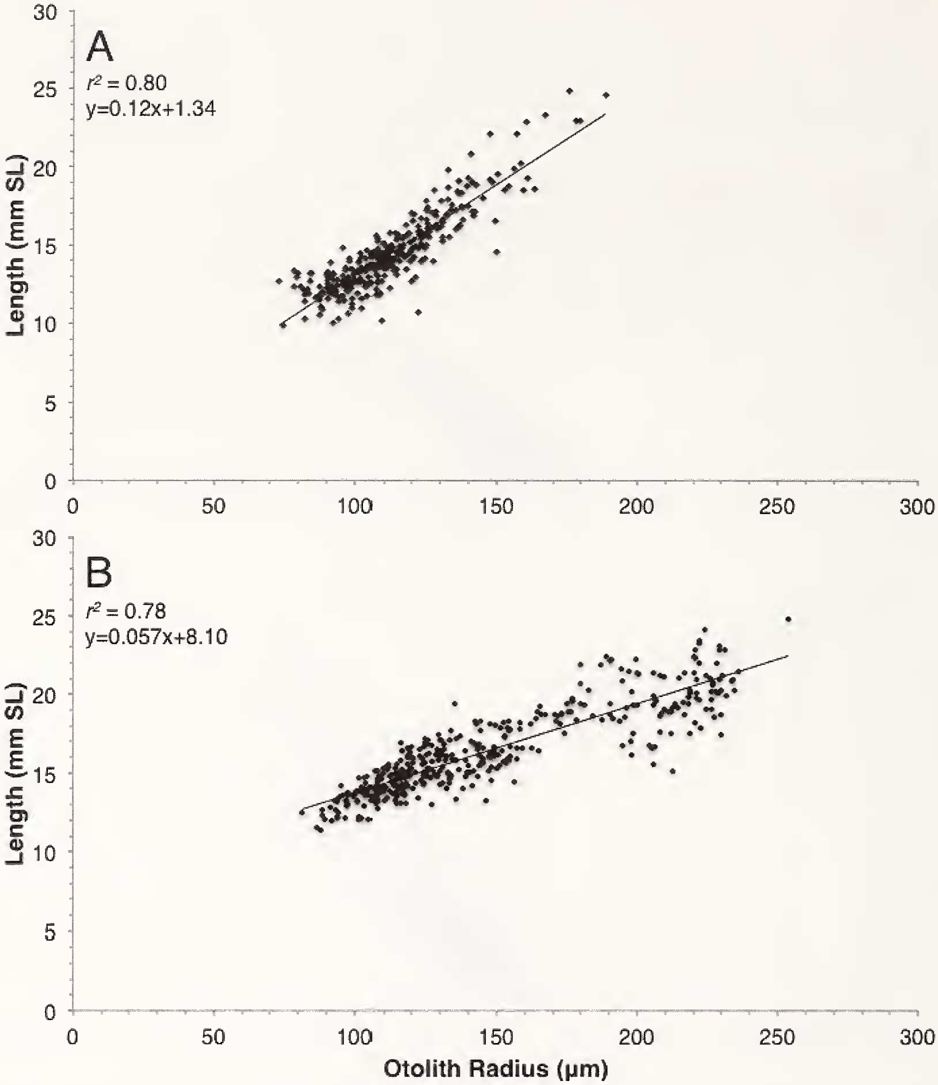

Fig. 6. Relationship between otolith radius and body length for the Arrow Goby (A) and Tidewater Goby (B).

Table 1. Estimated larval durations, settlement sizes (standard length), and growth rates of the Arrow Goby (*Clevelandia ios*) and Tidewater Goby (*Eucyclogobius newberryi*) pooled over all study sites (n = 8 and 10 study sites for the two species, respectively).

	Larval duration		Settlement		Growth rate	
Species	Range (days)	Mean ± SD (days)	Otolith radius (µm)	Length (mm)	Mean ± SD (µm/day^{-1})	N
E. newberryi	18 - 31	23.95 ± 2.71	75.62 ± 6.40	12.38 ± 0.36	2.86 ± 0.23	406
C. ios	20 - 33	26.11 ± 2.40	77.61 ± 6.37	10.00 ± 0.71	2.60 ± 0.22	317

did the Arrow Goby. It is likely that the Tidewater Goby has evolved the ability to settle and reach maturity faster than the Arrow Goby due to its shorter, annual life cycle.

Larval durations of other related goby species (e.g. *Gillichthys mirabilis*, *Ilypnus gilberti*, *Lepidogobius lepidus*, *Quietula y-cauda*), commonly referred to as the "bay gobies" (Teleostei: Gobionellidae) (Thacker 2009, Ellingson et al. 2014) have not yet been determined. In fact, detailed knowledge of early life history characteristics does not exist for many native fishes that occupy estuaries and wetlands in California. Larval traits have been studied more regularly in tropical gobies (Teleostei: Gobiidae), which on average, tend to exhibit more prolonged larval stages than those of the species in this study. Yamasaki and Maeda (2007) documented a 78-146 day larval duration in *Stiphodon percnopterygionus*, a stream-associated goby found in Okinawa Island, southern Japan. *Lentipes concolor*, an endemic Hawaiian amphidromous goby was found to have a larval duration between 63-106 days (Radtke et al. 2001). The goldspot goby (*Gnatholepis thompsoni*), commonly found on coral reefs in the Caribbean, was found to have a larval duration between 45-80 days (Samhouri et al. 2009), with the potential of reaching 112 days (Sponaugle and Cowen 1994). Another common goby in the Caribbean (*Coryphopterus glaucofraenum*), however, had a much shorter larval duration of 27 days (Sponaugle and Cowen 1994), similar to that found in this study for the Arrow Goby.

Previous estimates of larval characteristics of these two study species have varied widely, presumably due to methodological limitations. Estimates of larval duration for the Tidewater Goby have ranged from as little as several days (Capelli 1997) to a few weeks (Dawson et al. 2002). Past research on the Arrow Goby has provided a broad range of estimates of larval duration using both field collected and laboratory-reared specimens. However, none of these estimates were obtained from otolith analysis. Brothers (1975) estimated larval duration at approximately 30 days from the timing of annual reproduction and recruitment. Dawson et al. (2002) estimated a 2–4 week larval duration by extrapolating the time to reach 7 mm (10 days; Hart 1973) to the time to reach the average size at settlement of 13.1 $\pm$ 1.3 mm (range 10.0–16.6 mm) observed by Kent and Marliave (1997) for newly settled arrow gobies from British Colombia. Our back-calculated estimate of size at settlement (10.00 $\pm$ 0.6 mm) falls on the lower end of Kent and Marliave's (1997) range of size at settlement, but overlaps with measurements of nearshore postlarvae collected by Brothers (1975). Morphological descriptions of transitional juveniles (12.5 mm SL) from British Colombia are consistent with the morphology of juveniles in southern California estuaries that settled at a smaller size, perhaps indicating regional differences in size at settlement. It is possible, however, that some of these apparent differences in size at settlement are related to how fish were preserved in various studies, which can cause them to shrink (Hay 1982).

The larval traits investigated in this study varied among populations, possibly due to differences among estuaries in environmental conditions, such as temperature, water quality, or food resources. This could be one explanation for the different estimates of settlement size from this study, done in southern California, and that of Kent and Marliave (1997) conducted in British Colombia. Brothers (1975) found that the Arrow Goby lives for approximately one year in southern California, similar to the annual lifespan of the Tidewater Goby throughout its range, but has an extended lifespan in the more northern portions of its range (2-3 years). Swenson (1999) found that the average size of the Tidewater Goby was significantly larger in marsh habitats than in lagoons or creeks. She speculated that this was due to the more stable physical conditions of the marsh, which fosters improved growth, perhaps due to a more consistent or abundant supply of prey. It is also worth noting that, given genetic isolation of populations (e.g. Earl et al. 2010), adaptation to local conditions is also possible in the Tidewater Goby. Our findings provide baseline estimates of some of the early life history traits of the Tidewater Goby and the Arrow Goby, but these attributes are likely to vary with environmental parameters.

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